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Effects of face view discrimination learning on N170 latency and amplitude

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ABSTRACT

Learning is critical for fast and efficient object recognition. However, the neural implementation of object learning in the human brain remains largely unknown. Using combined psychophysics and electroencephalogram (EEG), we investigated the effects of perceptual learning on face processing. Human subjects were trained to discriminate face views at an in-depth face orientation (i.e. 30°) over eight daily sessions, which resulted in a significant improvement in sensitivity to the trained face view. Psychophysical results showed that this improvement was highly specific to the trained view. Before and after training, we recorded subjects' EEG signals responding to the trained and the untrained face views. Analyses of event-related potentials (ERPs) showed that face view discrimination training led to a larger reduction of N170 latency at the left occipital–temporal area with the trained face view, compared with the untrained ones. These findings provide evidence for the facilitation model on neuronal plasticity from visual experience, suggesting a faster processing speed of face induced by perceptual learning.

1. Introduction

Visual experience can improve detection and discrimination of elementary visual features, including contrast (Yu, Klein, & Levi, 2004), orientation (Schoups, Vogels, & Orban, 1995), spatial phase (Berardi & Fiorentini, 1987), stereoacuity (Fendick & Westheimer, 1983), hyperacuity (Fahle & Edelman, 1993), motion direction (Ball & Sekuler, 1987), and texture (Karni & Sagi, 1991). This process is referred to as perceptual learning and has been studied intensively in past decades because of its close links to cortical plasticity (Fahle, 2005; Gilbert, Sigman, & Crist, 2001; Sagi, 2011). Perceptual learning also occurs with complex visual stimuli. Psychophysical studies have demonstrated that object recognition and discrimination rely critically on learning (Furmanski & Engel, 2000; Golcu & Gilbert, 2009; Gold, Bennett, & Sekuler, 1999). For example, Bi et al. (2010) showed that face view (in-depth orientation) discrimination training could lead to a significant improvement in sensitivity to the trained face view orientation. This improved sensitivity was highly specific to the trained view and persisted up to 6 months. However, it is still far from fully understanding how perceptual learning affects object processing and representation in the brain.

Training subjects to recognize and discriminate objects is usually thought to induce changes in the strength and/or the selectivity of neuronal responses to those objects, but both functional magnetic resonance imaging (fMRI) and single-unit studies to date have generated contradictory and inconclusive results. On the one hand, several fMRI studies showed that object recognition or discrimination training generally increased neural response strength to the trained stimuli in ventral object-selective areas (e.g. fusiform cortex and lateral occipital cortex) (Gauthier et al., 1999; Grill-Spector et al., 2000; Jiang et al., 2007). On the other hand, neural responses in these ventral areas were found to decrease or did not change after object training (Gauthier et al., 2000; Harley et al., 2009; Op de Beeck et al., 2006; Yue, Tjan, & Biederman, 2006). Two monkey neurophysiological studies showed that neuronal selectivity for trained objects was remarkably enhanced after object discrimination training (Baker, Behrmann, & Olson, 2002; Logothetis, Pauls, & Poggio, 1995). Consistent with these findings, fMRI adaptation studies also suggested that training could narrow neuronal tuning in the lateral occipital cortex (Jiang et al., 2007; Yue, Tjan, & Biederman, 2006). However, other neurophysiological studies failed to find evidence of enhanced selectivity for trained objects. (Erickson, Jagadeesh, & Desimone, 2000; Vogels & Orban, 1994).

Another view regarding the effect of visual experience on object processing and representation is the facilitation model, which predicts that visual experience causes faster processing of stimuli, that is, shorter latencies or shorter durations of neural firing (Friston, 2005; Grill-Spector, Henson, & Martin, 2006). This model can be examined via single-unit recordings and/or EEG/MEG techniques. However, it has rarely been tested.

We carried out psychophysical and EEG experiments to investigate the effects of perceptual learning on face processing. Subjects

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were trained to discriminate face views at a face view orientation. Before and after training, EEG signals responding to the trained and the untrained face views were recorded. Analyses of event-related potentials (ERPs) were performed. We focused on the amplitude and latency of early ERP components (e.g. N170). The occipito-temporal N170 component is an established neural correlate of face processing, whose amplitude and latency can be significantly modulated by face perception (Rossion & Jacques, 2008). Our results show that perceptual learning led to a larger N170 latency reduction at the left occipital–temporal area, suggesting a faster processing speed of the trained face view.

2. Methods

2.1. Subjects

A total of seventeen naïve human subjects (nine male and eight female) participated in the experiment. They were right-handed with reported normal or corrected-to-normal vision and had no known neurological or visual disorders. Their ages ranged from 20 to 25. They gave written, informed consent in accordance with the procedures and protocols approved by the human subjects review committee of Peking University.

2.2. Stimuli and apparatus

A three-dimensional (3D) face model was generated by FaceGen Modeller 3.1. No hair was rendered. The model was the default average face (Fig. 1A) in the software and the value of texture gamma correction was set to 2. Face view images were generated by projecting the 3D face model with variant in-depth rotation angles onto the monitor plane with the front view (0°) as the initial position. Both left and right rotations were executed, with a step size of 0.2°. The stimuli extended $3^\circ \times 3^\circ$ of visual angle. They were presented on an IIYAMA HM204DT 22 inch monitor, with a spatial resolution of 1024×768 and a refresh rate of 100 Hz. Subjects viewed the stimuli from a distance of 60 cm. Their head position was stabilized using a chin rest and a headrest. Throughout the experiment, subjects were asked to fixate a small white dot presented at the center of the monitor.

2.3. Designs

The experiment consisted of three phases – pre-training psychophysical and EEG tests, face view discrimination training, and post-training psychophysical and EEG tests. We used QUEST staircase to measure face view discrimination thresholds, not only in psychophysical tests, but also in training (see below). During the training phase, each subject underwent eight daily training sessions to discriminate face views around the in-depth face orientation of 30°, either left tilted (−30°) or right tilted (+30°). A daily session (about 1 h) consisted of 25 QUEST staircases of 40 trials (Watson & Pelli, 1983). In a trial, 30° and $30^\circ \pm \theta^\circ$ face views were each presented for 200 ms and separated by a 600 ms blank interval (Fig. 1B). Their temporal order was randomized. Their spatial positions were randomly distributed within a $6.2^\circ \times 6.2^\circ$ area whose center was coincident with the fixation point, with a constraint that these two face views were separated by at least 1.5° of visual angle. Subjects were asked to make a 2-alternative-forced-choice (2-AFC) judgment of the orientation of the second face relative to the first face (left or right). A high-pitched tone was provided after a wrong response and the next trial began one second after response. The θ varied trial by trial and was controlled by the QUEST staircase to estimate subjects' face view discrimination threshold (75% correct).

During the pre- and post-training test phases, psychophysical and EEG tests were performed at face view orientations of −90°, −60°, −30°, 0°, 30°, 60° and 90° (Fig. 1A). We first measured face view discrimination thresholds at the seven views. Eight QUEST staircases (same as above) were completed for each view and each subject within 2 days. These seven view conditions were counterbalanced within individual subjects. Discrimination thresholds from eight staircases for each of the seven face views were averaged as a measure of subjects' discrimination performance, and then plotted as a function of view. Note that subjects were randomly selected to be trained at either −30° or +30°. Since training at the two views induced a similar learning effect, for the sake of presentation simplicity, the discrimination performance functions for subjects trained at −30° were flipped horizontally, and then averaged together with the functions for subjects trained at +30°. Subjects' performance improvement at a view was calculated as (*pre-training threshold* − *post-training threshold*)/*pre-training* threshold × 100%. To measure the time course of the training effect (learning curve), discrimination thresholds from 25 staircases in a daily training session were averaged, and then plotted as a function of training day. Learning curves were fitted with a power function (Jeter et al., 2009).

After acquiring psychophysical discrimination thresholds, we recorded EEG signals responding to the seven face views. The EEG test consisted of 35 blocks of 42 trials. Each block included six trials for each of the seven face views (totally 210 trials for each view). In a trial, two face views were each presented for 200 ms and separated by a 600 ms blank interval. Similar to the psychophysical test, subjects were asked to make a 2-AFC judgment of the orientation of the second face view relative to the first face view (left or right) by pressing one of two buttons with their left and right index fingers. The first face view was always one of the seven face views. The orientation difference (increment or decrement) between the first and the second face views was the discrimination threshold (75% correct) for the first face view measured in the psychophysical test. In a block, the order of the seven face views was randomized. Subjects were asked to blink as few as possible and they took a short break between blocks.

Prior to the experiment, subjects practiced four QUEST staircases (160 trials) for each face view to get familiar with the stimuli and the experimental procedure.

2.4. EEG recording and analysis

EEG was continuously recorded from 28 scalp electrodes that were mounted on an elastic cap according to the 10–20 system, including F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz and O2. The electrode at the right mastoid was used as on-line reference. Electrode impedance was kept below 5 kΩ. Eye blinks and vertical eye movement were monitored with electrodes located above and below the left eye. Horizontal electro-oculogram (EOG) was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. EEG was amplified with a gain of 500 K, bandpass filtered at 0.05–100 Hz. and digitized at a sampling rate of 1000 Hz. EEG epochs were made (see below) and referenced off-line to a common average reference (Rossion et al., 2000). Those epochs contaminated by eye blinks, eye movements, or muscle potentials exceeding ±50 μV at any electrode were excluded from further analysis.

EEG epochs beginning 200 ms before the onset of the first face stimulus in a trial and continuing for 600 ms were made. They were selectively averaged according to stimulus type (i.e. face view). The average waveforms were low pass filtered at 30 Hz and baseline corrected with respect to the mean voltage of the 200 ms pre-stimulus interval. The analysis focused on the peak

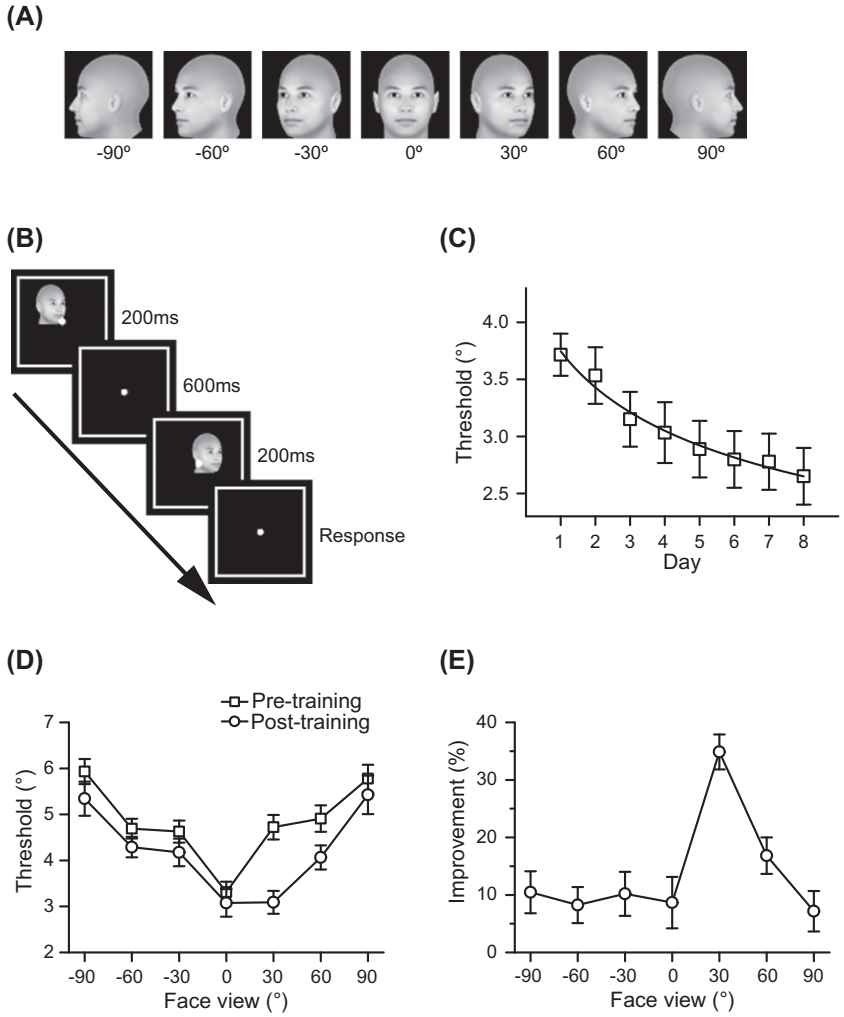

Fig. 1. Face view discrimination training resulted in a significant improvement in sensitivity to the trained face view. (A) Face views at seven orientations. Subjects were trained at the orientation of 30°. (B) Schematic description of a 2-AFC trial in a QUEST staircase for measuring face view discrimination thresholds. Two face views with a slight orientation difference were presented successively. Subjects were asked to make a 2-AFC judgment of the orientation of the second face relative to the first face (left or right). (C) Learning curve at the face view orientation of 30°. Face view discrimination thresholds are plotted as a function of training day. (D) Face view discrimination thresholds plotted as a function of face view before and after training. (E) Percent improvement in face view discrimination performance with seven face views after training. Data were averaged across 17 subjects. Error bars denote 1 SEM calculated across subjects.

amplitude and peak latency (relative to stimulus onset) of N170 and P1 at the occipito-temporal electrodes.

3. Results

3.1. Psychophysical results

We first measured subjects' face view discrimination thresholds at seven face view orientations of −90°, −60°, −30°, 0°, 30°, 60° and 90° (Fig. 1A and B). Then subjects practiced for 8000 trials during eight daily training sessions on face view discrimination at the face view orientation of 30°. Throughout the training course, their discrimination thresholds gradually decreased (Fig. 1C). After training, we measured thresholds at the seven orientations again.

Before training, subjects had a significant lower threshold (better performance) at 0° than the thresholds at other orientations (all $t(16) > 7.5, p < 0.01$) (Fig. 1D), which is consistent with the claim that three-dimensional symmetric shapes are discriminated more efficiently than asymmetric ones (Liu & Kersten, 2003). After training, the threshold at 30° was comparable to that at 0° ($t(16) = 0.09$, $p = 0.93$), and was significantly lower than those at other orientations (all $t(16) > 7.5, p < 0.01$) (Fig. 1D). We calculated the percent improvement in discrimination performance after training. The improvement with the trained face view was 35%, significantly higher than those (about 10%) with the untrained face views (Fig. 1E) (all $t(16) > 4.8, p < 0.01$). These results demonstrated a view-specific perceptual learning in face view discrimination, which replicated our previous finding (Bi et al., 2010).

3.2. ERP results

Since the occipito-temporal N170 component is an established neural correlate of face processing, our ERP analysis focused on N170 latency and amplitude. Fig. 2A shows the mean voltage topographies between 165 and 175 ms after the onset of the trained face view before and after training. Consistent with previous studies (Chen et al., 2009; Rossion & Jacques, 2008), the left and the right occipito-temporal areas (i.e. P7 and P8) exhibited the largest N170 responses to face images. Thus, ERP data analyses were performed with the peak amplitude and peak latency (relative to stimulus onset) of N170 at P7 and P8. An inspection of Fig. 2B revealed that, relative to the pre-training test, the amplitude of N170 reduced in

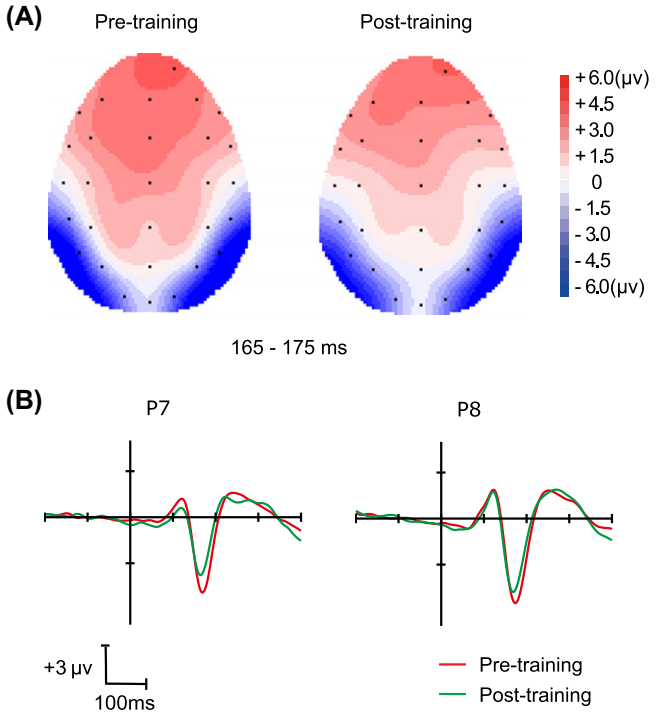

Fig. 2. (A) Mean voltage topographies between 165 and 175 ms after the onset of the trained face view before and after training. (B) Grand averaged ERPs at P7 and P8 evoked by the trained face view before and after training.

the post-training test. However, it was unclear if the reductions were due to the discrimination learning itself or some other factors (i.e. day-to-day measurement variance and stimulus repetition). To resolve this issue, we performed the following analyses to search for changes in peak amplitude and latency that were specifically related to the face view discrimination learning. For both electrodes, a repeated-measures analysis of variance (ANOVA) of peak amplitude and latency was performed with test (pre- and post-training tests) and face view (−90°, −60°, −30°, 0°, 30°, 60° and 90°) as within-subject factors. A main effect of test means a significant amplitude/latency difference between the pre- and post-training tests. An interaction effect between test and face view means that the difference varies significantly across face views. Since amplitude/latency differences with the untrained face views can be used to quantify the effects of day-to-day measurement variance and stimulus repetition, planned paired *t*-tests were run to compare amplitude/latency differences between the trained and the untrained face views. If the difference with the trained face view is significantly larger than those with the untrained face views, the difference should be specifically related to the face view discrimination learning.

Fig. 3 shows N170 amplitudes and latencies at P7 and P8 in the pre- and post-training tests and their differences between the two tests. For N170 amplitude, a significant main effect of test was found at P7 ($F(1,16) = 6.46$, $p = 0.02$), but not at P8. The amplitude reduced in the post-training test compared to the pre-training test. P7 also showed a significant interaction ($F(6,96) = 2.31$, $p = 0.04$). However, further planned paired *t*-tests showed that the amplitude reduction with the trained view was significantly larger than only one or two untrained views (i.e. 0° and −90°).

For N170 latency, a significant main effect of test was found at P7 ($F(1,16) = 16.11$, $p = 0.001$), but not at P8. The latency reduced in the post-training test compared to the pre-training test. The reductions for the −90°, −60°, −30°, 0°, 30°, 60° and 90° views were 4, 2, 3, 5, 7, 4 and 4 ms respectively. P7 also showed a significant interaction ($F(6,96) = 3.49$, $p = 0.004$). Further planned paired *t*-tests showed that, at P7, the latency reduction with the trained view was significantly larger than those with all untrained views (all $t(16) > 2.31$, $p < 0.05$). These results suggest that the latency reduction (not amplitude reduction) of N170 at the left occipito-temporal area was highly specific to the trained face view. We next examined the relationship between the latency reduction at P7 and discrimination performance improvement with the trained view; no reliable correlation across subjects was found ($p = 0.16$).

To overcome unit issues for making a direction comparison between latency reduction and amplitude reduction, we calculated the percentage by which the latency reduction or the amplitude reduction with the trained view was larger than that with the untrained views. We found, at P7, the latency reduction with the trained view was 69% larger than that with the untrained views, and the amplitude reduction with the trained view was only 7% larger than that with the untrained views. There was a significant difference between the percentages (69% vs. 7%, $t(16) = 2.67$, $p = 0.017$). But we did not find a significant difference at P8.

The P1 (or P100) is an earlier component than the N170, peaking at around 100 ms after stimulus onset. It is thought to originate from striate and extrastriate visual areas (Di Russo et al., 2002). Previous studies (Goffaux, Gauthier, & Rossion, 2003; Itier & Taylor, 2004a) have reported larger P1 in response to faces than to objects, which might imply a face-selective characteristic of this component. Thus, we performed a similar statistical analysis with the amplitude and latency of the P1. We did not find any effect specific to the trained face view.

4. Discussion

We showed that, intensive face view discrimination training led to a larger N170 latency reduction at the left occipital–temporal area with the trained face view, relative to the untrained ones. However, we did not find a significant N170 amplitude change specific to the trained face view. Although several fMRI studies (Gauthier et al., 1999; Harley et al., 2009; Jiang et al., 2007; Op de Beeck et al., 2006) have been performed to investigate how perceptual learning affects object representation, EEG technique has an excellent temporal resolution, allowing inferences regarding time-course differences in visual processing that arise as a consequence of training.

The occipito-temporal N170 enjoys an important and unique status in face studies and is considered a neurophysiological correlate of face perception. This face-specificity view of the N170 is mainly supported by two findings. One is that the amplitude of the N170 is systematically larger to faces than to other object categories (Bentin et al., 1996; Itier & Taylor, 2004a). The other is that the N170 is enhanced and delayed specifically by face inversion (Rossion et al., 2000), a manipulation that impairs face identification probably by disrupting configural processing (face inversion effect, Yin, 1969). In this study, although we found a reduction of N170 amplitude in the post-training test compared to the pre-training test, the reduction was not specific to the trained face view, which does not provide evidence for that perceptual learning can alter the strength of neuronal responses at population level to those trained objects. It is possible that the negative results for the amplitude analysis might be due to the limited number of subjects. But indeed, there is not much difference in N170 amplitude reduction between the trained and untrained face views (see Fig. 3). The only significant change associated with the view-specific learning was the N170 latency reduction. Many studies have demonstrated that N170 latency is closely correlated with the processing speed of face (Itier & Taylor, 2004b; Jacques & Rossion, 2007; McCarthy et al., 1999). On one hand, face inversion and face contrast reversal

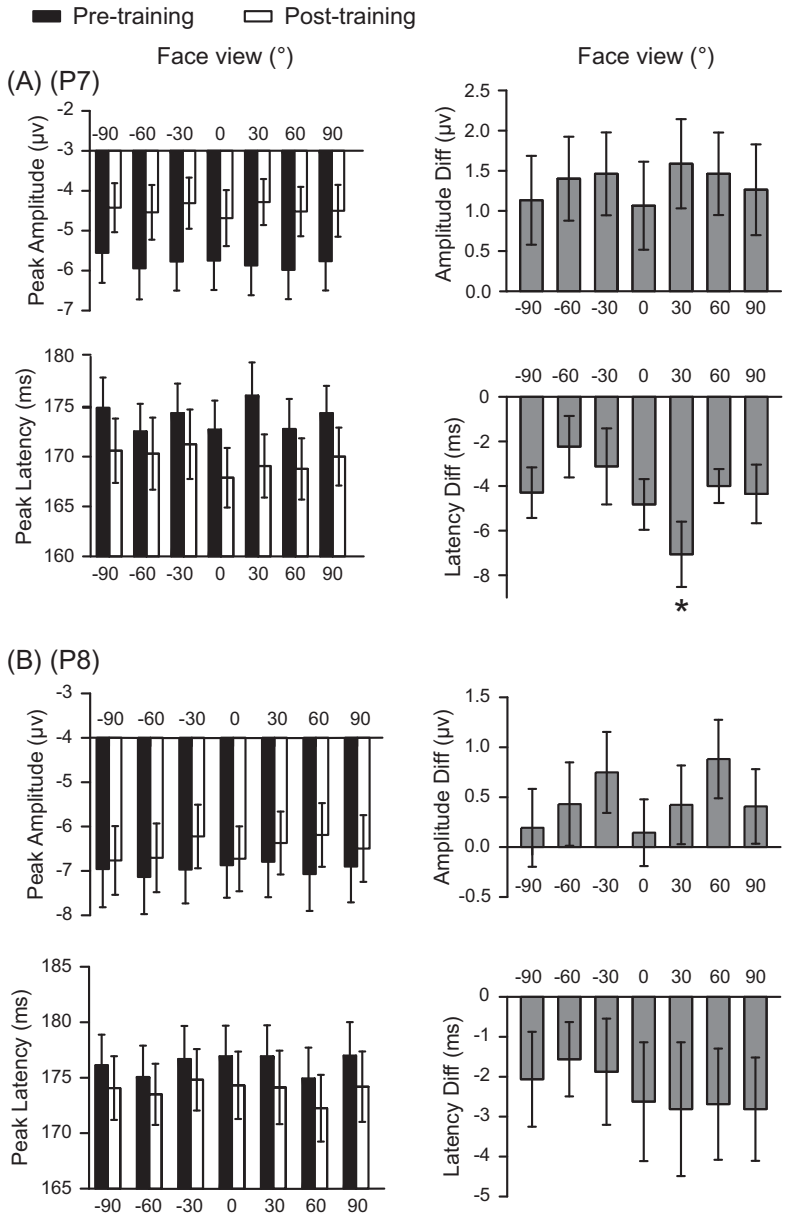

Fig. 3. Amplitudes and latencies of N170s evoked by seven face views before and after training and their differences at P7 (A) and P8 (B). Asterisk indicates a statistically significant difference between the trained and untrained face views. Error bars denote 1 SEM calculated across subjects.

are well known to impair face perception by disrupting configural information at the encoding stage of face processing. It has been shown that both of them led to delayed behavioral response and N170 (Itier & Taylor, 2004b; Jacques & Rossion, 2007). On the other hand, face repetition priming could speed up behavioral response and shorten N170 latency (Itier & Taylor, 2004b). Thus, our ERP results suggest that discrimination learning induced a faster speed of face processing. Indeed, Posner, DiGirolamo, and Fernandez-Duque (1997) have suggested that priming and perceptual learning are two possible versions of the same process of automaticity, which share underlying neuronal mechanisms. Although we did not measure subjects' behavioral response speed quantified by reaction time, this suggestion is consistent with their subjective report that, after training, they could extract face configural information from the trained view more quickly and easily. Note that the face stimuli were presented only with 200 ms and their spatial positions were randomized within an area.

The finding of the N170 latency reduction after training provides evidence for the facilitation model, which predicts that visual experience causes faster processing of stimuli, that is, shorter latencies or shorter durations of neural firing (Friston, 2005; Grill-Spector, Henson, & Martin, 2006). The model assumes that the cause of this faster processing is synaptic potentiation between neurons following visual experience, and that this potentiation can occur at many levels in the processing stream. Consequently, information flows through the stream more rapidly, and hence identification of a trained stimulus occurs faster (Grill-Spector, Henson, & Martin, 2006). Of course, the faster processing speed can be viewed as a result of improved sensitivity after training (Sterkin, Sterkin, & Polat, 2008).

Another interesting finding related to the N170 latency is that the view-specific N170 latency effect was found only at the left occipital–temporal area (e.g. P7), but not the right occipital–temporal area (e.g. P8). The right hemisphere dominance in face processing has been documented in literature for a long time (Gazzaniga & Smylie, 1983). N170 is also well known for its right lateralized topographical distribution on occipital–temporal sites (Rossion & Caharel, 2011). It is typically larger at P8 than at P7

(see Fig. 2). However, Grill-Spector and colleagues (2004) showed that both left and right FFA (fusiform face area) activities were correlated with face recognition. To date, we still do not know much about the functional difference between the two hemispheres in face processing. Our data suggest that the left hemisphere (e.g. left FFA) is more susceptible to perceptual learning and more plastic, which is in accordance with the finding that training with novel objects (i.e. Greebles) led to a left-lateralized facelike N170 response (Rossion et al., 2002).

We did not find a significant correlation across subjects between the latency reduction at P7 and discrimination performance improvement with the trained view. There are two possible explanations. One is that ERP technique is not sensitive enough to detect individual difference, especially for a small group of subjects (Bao et al., 2010). Thus, in future study, it would be interesting to see if a significant correlation can be found with a larger group of subjects. The other explanation is that almost all subjects in the present study are strong learners. If we have included some weaker learner (thus increased the range of performance improvement), we might have a better chance to find a significant correlation (see Censor et al., 2009).

We believe that our results cannot be explained by other factors (e.g. attention, task difficulty, eye movement). During the pre- and post-training EEG recording periods, subjects performed the same discrimination task as that during training (see Section 2). There was no significant difference in subjects' discrimination performance between the pre- and post-training tests (both were about 75% correct), suggesting no difference in task difficulty and (presumably) attention. In our study, subjects were asked to fixate a small white dot throughout the experiment. The latency of miniature saccade is usually larger than 200 ms (Yuval-Greenberg et al., 2008). Our data analysis focused on the ERP components between 100 and 200 ms after stimulus onset, which cannot be due to miniature saccade.

In summary, perceptual learning of face view discrimination led to a larger reduction of N170 latency at the left occipital–temporal area with the trained face view, compared with the untrained ones. These findings provide evidence for the facilitation model on neuronal plasticity from visual experience, suggesting a faster processing speed of face induced by perceptual learning.

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References

Baker, C. I., Behrmann, M., & Olson, C. R. (2002). Impact of learning on representation of parts and wholes in monkey inferotemporal cortex. *Nature Neuroscience, 5*, 1210–1216.

Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research, 27*, 953–965.

Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. *Journal of Neuroscience, 30*, 15080–15084.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*, 551–565.

Berardi, N., & Fiorentini, A. (1987). Interhemispheric transfer of visual information in humans: Spatial characteristics. *Journal of Physiology, 384*, 633–647.

Bi, T., Chen, N., Weng, Q., He, D., & Fang, F. (2010). Learning to discriminate face views. *Journal of Neurophysiology, 106*, 3305–3311.

Censor, N., Bonneh, Y., Arieli, A., & Sagi, D. (2009). Early vision brain responses which predict human visual segmentation and learning. *Journal of Vision, 9*(4), 12, 1–9.

Chen, J., Liu, B., Chen, B., & Fang, F. (2009). Time course of amodal completion in face perception. *Vision Research, 49*, 752–758.

Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping, 15*, 95–111.

Erickson, C. A., Jagadeesh, B., & Desimone, R. (2000). Clustering of perirhinal neurons with similar properties following visual experience in adult monkeys. *Nature Neuroscience, 3*, 1143–1148.

Fahle, M. (2005). Perceptual learning: Specificity versus generalization. *Current Opinion in Neurobiology, 15*, 154–160.

Fahle, M., & Edelman, S. (1993). Long-term learning in Vernier acuity: Effects of stimulus orientation, range and of feedback. *Vision Research, 33*, 397–412.

Fendick, M., & Westheimer, G. (1983). Effects of practice and the separation of test targets on foveal and peripheral stereoacuity. *Vision Research, 23*, 145–150.

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences, 360*, 815–836.

Furmanski, C. S., & Engel, S. A. (2000). Perceptual learning in object recognition: Object specificity and size invariance. *Vision Research, 40*, 473–484.

Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience, 3*, 191–197.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects. *Nature Neuroscience, 3*, 568–573.

Gazzaniga, M. S., & Smylie, C. S. (1983). Facial recognition and brain asymmetries: Clues to underlying mechanisms. *Annals of Neurology, 5*, 536–540.

Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron, 31*, 681–697.

Goffaux, V., Gauthier, I., & Rossion, B. (2003). Spatial scale contribution to early visual differences between face and object processing. *Cognitive Brain Research* (16), 416–424.

Golcu, D., & Gilbert, C. D. (2009). Perceptual learning of object shape. *Journal of Neuroscience, 29*, 13621–13629.

Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Signal but not noise changes with perceptual learning. *Nature, 402*, 176–178.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences, 10*, 14–23.

Grill-Spector, K., Knouf, N., & Kanwisher, N. G. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience, 7*, 555–562.

Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nature Neuroscience, 3*, 837–843.

Harley, E. M., Pope, W. B., Villablanca, J. P., Mumford, J., Suh, R., Mazziotta, J. C., et al. (2009). Engagement of fusiform cortex and disengagement of lateral occipital cortex in the acquisition of radiological expertise. *Cerebral Cortex, 19*, 2746–2754.

Itier, R. J., & Taylor, M. J. (2004a). Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs. *Neuroimage, 21*, 1518–1532.

Itier, R. J., & Taylor, M. J. (2004b). N170 or N1? Spatiotemporal differences between object and face processing using ERPs. *Cerebral Cortex, 14*, 132–142.

Jacques, C., & Rossion, B. (2007). Early electrophysiological responses to multiple face orientations correlated with individual discrimination performance in humans. *Neuroimage, 36*, 863–876.

Jeter, P.E., Dosher, B.A., Petrov, A., & Lu, Z. (2009). Task precision at transfer determines specificity of perceptual learning. *Journal of Vision, 9*(3), 1, 1–13.

Jiang, X., Bradley, E., Rini, R. A., Zeffiro, T., VanMeter, J., & Riesenhuber, M. (2007). Categorization training results in shape- and category-selective human neural plasticity. *Neuron, 53*, 891–903.

Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America, 88*, 4966–4970.

Liu, Z., & Kersten, D. (2003). Three-dimensional symmetric shapes are discriminated more efficiently than asymmetric ones. *Journal of the Optical Society of America A, 20*(7), 1331–1340.

Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Current Biology, 5*, 552–563.

McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception: II. Response properties of face-specific potentials generated in occipitotemporal cortex. *Cerebral Cortex, 9*, 431–444.

Op de Beeck, H. P., Baker, C. I., DiCarlo, J. J., & Kanwisher, N. G. (2006). Discrimination training alters object representations in human extrastriate cortex. *Journal of Neuroscience, 26*, 13025–13036.

Posner, M. I., DiGirolamo, G. J., & Fernandez-Duque, D. (1997). Brain mechanisms of cognitive skills. *Consciousness and Cognition, 6*, 267–290.

Rossion, B., & Caharel, S. (2011). ERP evidence for the speed of face categorization in the human brain: Disentangling the contribution of low-level visual cues from face perception. *Vision Research, 2011*, 1297–1311.

Rossion, B., Gauthier, I., Goffaux, V., Tarr, M. J., & Crommelinck, M. (2002). Expertise training with novel objects leads to left-lateralized facelike electrophysiological responses. *Psychological Science, 13*, 250–257.

Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., et al. (2000). The N170 occipitotemporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in human brain. *NeuroReport, 11*, 69–74.

Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage, 39*, 1959–1979.

Sagi, D. (2011). Perceptual learning in vision research. *Vision Research, 51*, 1552–1566.

Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology, 483*, 797–810.

Sterkin, A., Sterkin, A., & Polat, U. (2008). Response similarity as a basis for perceptual binding. *Journal of Vision, 8*(7), 17, 1–12.

Vogels, R., & Orban, G. A. (1994). Does practice in orientation discrimination lead to changes in the response properties of macaque inferior temporal neurons? *European Journal of Neuroscience, 6*, 1680–1690.

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics, 33*, 113–120.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology, 81*, 141–145.

Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision, 4*, 169–182.

Yue, X., Tjan, B., & Biederman, I. (2006). What makes faces special? *Vision Research, 46*, 3802–3811.

Yuval-Greenberg, S., Tomer, O., Keren, A. S., Nelken, I., & Deouell, L. Y. (2008). Transient induced gamma-band response in EEG as a manifestation of miniature saccades. *Neuron, 58*, 429–441.